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Forage species in predator diets: Synthesis of data from the California Current

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ABSTRACT

Characterization of the diets of upper-trophic pelagic predators that consume forage species is a key ingredient in the development of ecosystem-based fishery management plans, conservation of marine predators, and ecological and economic modeling of trophic interactions. Here we present the California Current Predator Diet Database (CCPDD) for the California Current region of the Pacific Ocean over the past century, assimilating over 190 published records of predator food habits for over 100 predator species and 32 categories of forage taxa (species or groups of similar species). Literature searches targeted all predators that consumed forage species: seabirds, cetaceans, pinnipeds, bony and cartilaginous fishes, and a predatory invertebrate. Diet data were compiled into a relational database. Analysis of the CCPDD highlighted differences in predator diet data availability based on geography, time period and predator taxonomy, as well as prominent prey categories. The top 5 forage taxa with the most predators included juvenile rockfish, northern anchovy, euphausiid krill, Pacific herring and market squid. Predator species with abundant data included Pacific hake, common murre, and California sea lion. Most diet data were collected during the summer; the lack of winter data will restrict future use of the CCPDD to understand seasonal patterns in predator diet unless more such data become available. Increased synthesis of historical information can provide new resources to understand patterns in the role of forage species in predator diet. Increased publication and/or accessibility of long-term datasets and data-sharing will further foster the synthesis of information intended to inform the management, conservation and understanding of marine food webs.

1. Introduction

Ecosystems are complex systems in which small-scale interactions may shape large-scale processes (Cowan et al., 2012; Levin and Lubchenco, 2008). In marine ecosystems this complexity may limit the understanding of food web dynamics and predator-prey interactions (Frid et al., 2006). For example, forage fish fisheries account for over 30% of marine landings globally (Alder et al., 2008), but knowledge is limited on how removals of these fish affect marine ecosystem functions (Pikitch et al., 2014; Smith et al., 2011). Food web models that examine the impacts of forage fisheries on marine ecosystems rely on detailed information on predator food habits and diet composition, information that is rarely available at the desired high-resolution spatial and temporal scales. Spatial details are needed to account for large-scale delineation of bio-physical features (Fujioka et al., 2014; Sherman, 1995). Temporally explicit data provide key information on seasonal or inter-annual variation that can affect predators via changes in prey energetic content (Rojbek et al., 2014) or prey availability (Ainley et al., 1996; Becker et al., 2007). Importantly, when data are averaged across space and time the reduced resolution can mask high local diet dependencies (Pikitch et al., 2014). Thus, enhancing knowledge of spatial and temporal detail in pelagic food webs is required to improve our abilities to assess forage fisheries, as well as climatic impacts, within and across marine ecosystems.

In contrast to many marine ecosystems, information on food habits and diet composition of marine middle- and upper-trophic-level predators in the California Current System (CCS) is rich. In this ecosystem, observational studies of pelagic predator diets have been conducted over the past 100 years, but assimilation of this information in food web models has been hindered by: 1) the high species diversity of middle- to upper-trophic-level predators (>160 species) that eat a diversity of forage species, 2) the large spatial domain of the CCS that spans Canada, the United States, and Mexico, and 3) the relatively short-term nature of the majority of these studies. To address the need for greater spatial and temporal detail for inclusion in ecosystem models of the CCS, we designed and populated the *California Current Predator Diet Database* (CCPDD). In this paper, we describe the database,

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identify gaps in food web knowledge, and review how we compiled disparate information from the peer-reviewed and technical literature to enhance understanding of food webs in this region. To meet this objective, we compiled existing research on predators of 32 focal taxa, expanding the traditional definition of small schooling pelagic fishes to include invertebrate taxa <50 cm in length and juvenile stages of larger fishes, which are also important components of predator diet in this system. We assessed the limitations of this synthesis in taxonomic, spatial, and temporal terms, as well as the use of different measurement units for predator consumption. With this database, we address the following questions: 1) Which forage species are commonly eaten by upper-trophic-level pelagic predators in the CCS? 2) What is the taxonomic, spatial, and temporal resolution of data on various forage species in predator diets?

2. Methods

2.1. Literature search and selection

We conducted a systematic review of the literature by querying the BIOSIS search engine for articles on predators occurring in the CCS from the northern tip of Vancouver Island, Canada, to the southern tip of Baja California, Mexico. Queries included topical keywords for diet and CCS geography, and taxonomic terms for each major taxonomic group of predators (Table 1). For bony fishes, taxonomic searches were for families and genera of marine fish known in the CCS (Eschmeyer and Herald, 1983), including both current and synonymous taxonomic names (based on the Integrated Taxonomic Information System [ITIS]).

Paper titles and abstracts returned from the search were screened by multiple expert reviewers (Table 1) to include only those with 1) middle- or upper-trophic-level predators, 2) CCS geographic region[1] (nearshore to ~200 nmi offshore, Baja to Vancouver Island), 3) indicator forage taxa identified to species, genus or family (those not denoted by * in Table 2), and 4) numerical or proportional diet data (e.g., not raw fatty acid data, and rarely stable isotope data). This list was supplemented by "citation chasing" (searching within existing articles, reviews, and books to avoid "availability bias", or including only easily-available studies; Collaboration for Environmental Evidence, 2013, p. 41), and querying subject experts for different taxonomic groups, Google's online search engine, subject-specific databases (Washington Seabird Diet Database, S. Pearson/WDFW; Northern CCS Fish Diet Database, R. Brodeur/NMFS), and government websites (National Oceanographic and Atmospheric Association, National Marine Fisheries Service, Canadian Department of Fisheries and Oceans, and state wildlife management departments). This screening sequence returned 285 relevant citations (Appendix A).

We entered data from 193 of the relevant citations in peer-reviewed journal publications and books (n = 161), technical reports (n = 19), and theses (n = 13). We prioritized data entry to achieve a broad perspective on predator diet, but could not enter every citation given time limitations. First we entered a minimum of one citation for each predator species, then we included as many regions as data were available for each predator (Canada, Washington, Oregon, northern California, central California, southern California, Mexico), and finally we filled in temporal gaps where possible with at least one citation for more recent data from the year 2000 forward. Additionally, we entered as much data as were available for those predators and prey with limited diet data (e.g., cetaceans as predators, sardines as prey). This approach ensured we had strong taxonomic, spatial and temporal resolution for predator diet. Of the remaining 92 citations not in the database, 75 were filed for future use because some data for the predator had already been entered in each region for the more recent time period or because data from a time-series was redundant with a more recent citation. The remaining 17 citations were either impossible to locate by interlibrary loan, or were acquired after analysis began.

The exclusion of additional citations due to time limitations was primarily for well-studied predators with many citations, e.g., for common predators in regions or time periods already represented in the CCPDD, including salmon, Pacific cod, Pacific hake, Caspian tern, Cassin's auklet, common murre, pigeon guillemot, rhinocerous auklet, California sea lion, and harbor seal. Supplements 1 and 2 provide a grid that portrays the citations included in the CCPDD, highlighting excluded citations that overlap in time (Supplement 1) and space (Supplement 2), as well as those not entered because the data were collected prior to 2000 or the citation was not yet published or difficult to locate. This first version of the CCPDD was developed to include broad scale spatial representation of diet data for each predator species, with an emphasis on more recent data from 2000 forward. Future iterations of the project will focus on entering newly published datasets, and enhancing the spatio-temporal resolution for data-rich predator species. In order to capture the best possible representation of which predators consume forage taxa among different regions, we occasionally include data from beyond the boundaries of the CCS (e.g., inland seas), when it improves the resolution of the diet data. We feel the benefits of characterizing the potential for consumption of forage taxa outweigh the cost of including data from slightly outside the CCS domain. For example, although lingcod occurs throughout the CCS, the only published diet data in WA comes from Puget Sound (Beaudreau and Essington, 2007). Likewise, the only copper rockfish, and coho and chum salmon diet data available in Canada are from inlets in British Columbia (Murie 1995, King and Beamish, 2000). When seabird colonies occur slightly inland, such as Caspian terns near the mouth of the Columbia River (e.g., Roby et al., 2002), an inference of at-sea foraging from diet composition supports inclusion in the database. Data from these studies are valuable because they improve geographic variation in diet data for predators otherwise lacking information in individual regions or in some cases at all. Future analyses can query the CCPDD for studies from varying spatial areas.

2.2. Database structure and data entry

We developed the database by reviewing each citation to characterize the range of methodological information (e.g., consumption unit types, predator metadata, prey metadata) and used this list to build a web-based data-entry form as well as database tables. Data were extracted by annotating PDF files and the data were entered just as they occurred in the citation (i.e., numeric quantities were not transformed, used given taxonomic names). Graphical data were extracted with GraphClick (Arizona Software, 2010) when original data could not be obtained directly from the text. The relational database stores individual occurrences of a predator eating a prey. Each record includes information on the citation, study location, study date, observation type (e.g., stomach content, visual observation), predator (taxonomy, life-history stage, sample size), and prey (taxonomy, life-history stage, amount consumed (e.g., percent mass, number, or frequency of occurrence; or non-proportional data)). Location information was extracted from written descriptions and maps in the original text and was entered by drawing polygons in a Geographic Information System (QGIS Development Team, 2013; Szoboszlai et al., 2015). Additional information housed in the database but not included here will be reported in future publications and includes: study time of day, study depth, predator size/age/sex, prey size/age/sex, and values for the amount of prey consumed.

[1] For a few wide-ranging predator species we included data from the Eastern Tropical Pacific, North Pacific, inland seas, river mouths, and Gulf of California due to limited data from the CCS (annotated in Appendix B).

Table 1
Literature search terms and results. TS = topic, TA = taxonomic designation. Citation Screening Sequence details the process of refining the literature search.

Diet keywords		Geographic keywords		Taxonomic data keywords	Taxonomic group name	Citation screening sequence	Number of citations entered (known)[b]
TS = (diet* OR stomach* OR "stable isotope*" OR "food habit*" OR trophic* OR prey OR food* or feed*)	AND	TS = ("California Current" OR Mexico OR Baja OR California OR Oregon OR Washington OR "British Columbia")	AND	TA = Family & Genus level names	Bony Fishes	Keyword search (2548 citations); expert review of titles/abstracts (383 citations); full text review of forage in diet and citation chasing (287 citations, final count)[a]	37 (68)
				TA = (Chondrichthyes)	Cartilaginous Fishes		18 (24)
				TA = (Anseriformes OR Charadriiformes OR Gaviiformes OR Pelecaniformes OR Phaethontiformes OR Podicipediformes OR Procellariiformes)	Seabirds		77 (99)
				TA = (Cetacea)	Cetaceans		31 (38)
				TA = (Phocidae OR Otariidae)	Pinnipeds		35 (67)
				TA = (Dosidicus gigas)	Humboldt Squid		3 (3)

[a] Note the sum for the 'Number of Citations Entered (Known)' column (299) is greater than the final citation count (287) indicated here because some citations included data for mutliple taxonomic groups, i.e. fishes, pinnipeds and cetaceans.
[b] Seabirds have the highest number of citations entered because seabird predator diet was reported for single species in individual citations, whereas other taxa had multiple species reported within one citation.

2.3. Technical validation

We assessed the accuracy of the data entered both during and after the process of populating the database (Lindquist, 2004; Twidale and Marty, 1999). To begin, we developed a structured data model with predefined lists of values that built in syntactic accuracy, thereby reducing the level of user judgment necessary to enter data, limiting user-based errors, and assuring consistency among data records. We synchronized taxonomic information with ITIS, a United States government database that provides access to standardized nomenclature and reliable information on hierarchical classification and species names. The data entry interface incorporated user input during the building phase to ensure high-quality data and functionality. Data entry was limited to two trained researchers and one supervisor who entered the majority of data including more difficult to interpret data; these methods avoid input errors due to misconception. Post-hoc data verification methods assured we met data quality objectives of a <5% error rate (Twidale and Marty, 1999) for the value of a database field. We used both implicit and explicit post-hoc methods for error detection. The former was an opportunistic approach, whereby errors discovered during regular use of the database led to the discovery of other similar errors; the latter a systematic, manual comparison of 5% of the total data records (711 of 14,219 predator-prey links) with original citations, yielding an error rate of 4.2% (30 of 711 records reviewed).

2.4. Query design

Initially, taxonomic updates were executed by converting outdated names to current names based on information stored in ITIS, allowing for all output data to be taxonomically equivalent. Then we appended the list of candidate forage taxa used in the literature search by querying all prey taxa in the database, and using the following criteria to define a prey taxa as forage if it: 1) is widely eaten (comprised >10% of the diet of >10 predator species), 2) is small in size (ranging from 1-50 cm), 3) occupies a low trophic level (eats small planktivorous species < 2 cm in length), 4) has aggregative or schooling behavior and is pelagic/non-benthic during the life history phase of interest (e.g., juvenile rockfish are pelagic), and 5) inhabits a geographic range primarily within the CCS (e.g., range is not primarily estuarine/offshore or sub-tropical/sub-arctic) (Table 2). Next we extracted from the database any record of a predator eating a forage taxon; all remaining prey species were excluded from the analysis. Then we subset the records to just predators whose: 1) habitat was pelagic (not exclusively benthic), and 2) geographic range was primarily within the CCS (not restricted to the northern/southern edge of the CCS) and overlaps at least partially with the continental shelf.

When appropriate, forage categories were grouped and queried at a higher taxonomic level, due to difficulty in identifying some taxa to species (i.e. rockfish and sanddabs at the genus level; right-eye flounders, lanternfish, sculpins, gonatid squid, surf perches, and smelts at the family level). In diet analysis, the identification of some taxa beyond genus level can be limited because it requires expert knowledge, or cannot be resolved (e.g., juvenile rockfish are difficult to identify by otolith; visual observations of seabird diet occur from long distances). Therefore, comparison among forage groups must consider the effect of compiling information at different taxonomic levels: individual forage species with high numbers of predators represent an approximation of the maximum number of predators, whereas forage species grouped at the genus level or higher may have inflated numbers of predators, but this value cannot be resolved due to limitations of how the raw data were collected.

2.5. Data output

The predator-prey interactions output by these queries were summarized by both forage prey taxa and per predator taxa. Forage taxa were ranked by total number of predators, supplemented by detail on number of citations, number of predator samples examined, and number of predator-prey links. For predators, we summarized consumption by major taxonomic group (e.g., pinnipeds, cetaceans, seabirds) by observation type, season, year, prey consumption units, and availability of regional data. More specific detail was compiled for individual predator species and includes special status designation, cumulative sample size, observation type, number of predator-prey links, number of citations, number of geographic regions in the species' range with data, year and season of observations, and types of consumption units.

We also assessed how well the database represents the complete set of predators in the CCS who consume forage species by identifying potential predators lacking published diet data. We obtained lists of potential predators from expert assessment of middle- to upper-trophic predators that are primarily pelagic with forage species in the diet, occur geographically within the CCS, and are regular residents of the system (i.e., not transients occurring in small numbers). For seabirds we consulted checklists, results of at-sea surveys, and range maps (Briggs et al., 1987; CalCOFI, 2008; Dunn and Alderfer, 2006, NMFS data, Line P data (Fisheries and Oceans Canada), Cornell Lab of Ornithology, 2014). For fishes we reviewed the list of CCS predators at fishbase.org (Froese and Pauly, 2015), selected

Table 2
Forage categories and summaries of their occurrence in the database, arranged by descending number of predators and grouped to highlight breaks in the data based on cumulative percentage for number of predators eating different prey taxa (highest (51–61 predators), high (32–41), intermediate (21–30), low (11–18)).

Prey Category Scientific Name	Prey Common Name	Number of Predators	Number of Predator Samples[d]	Number of Citations w/ Prey in Diet	Number of Predator-Prey Links[e]	Prey Size[f]	Forage Group[g]	Prey Size Type
Sebastes spp.	rockfishes	61	-	97	616	9 cm[f,h]	juv	set.
Engraulis mordax[a]	northern anchovy	57	92,479	91	493	23 cm[i]	sp	max
Euphausiacea	krill	56	-	66	1,078	3 cm[j]	i	max
Clupea pallasii[a]	Pacific herring	52	103,019	85	395	46 cm[i]	sp	max
Loligo opalescens	market squid	51	59,821	69	386	20 cm[k]	i	max
Pleuronectidae[a]	righteye flounders	41	-	58	328	6 cm[l]	juv	max juv
Myctophidae	lanternfishes	40	-	39	328	40 cm[l]	sp	max
Cottidae	sculpins	40	-	60	230	2 cm[l]	juv	trans.
Citharichthys spp.[a]	sanddabs (lefteye flounder)	39	-	46	149	5 cm[f,l]	juv	max juv
Gonatidae[b]	gonatid squid	38	-	43	171	42 cm[m]	i	max
Embiotocidae	surfperches	37	-	63	302	47 cm[i]	sp	max
Merluccius productus	Pacific hake	35	46,471	64	234	4 cm[f,l,n]	juv	trans.
Cololabis saira	Pacific saury	34	22,751	39	198	36 cm[i]	sp	max
Osmeridae	smelts	33	-	62	402	25 cm[i]	sp	max
Sardinops sagax[a,c]	Pacific sardine	32	22,936	43	190	41 cm[i]	sp	max
Ammodytes hexapterus	Pacific sandlance	32	102,399	56	230	20 cm[i]	sp	max
Cancridae	rock crabs	30	-	20	139	1 cm[o]	i	larval size
Gadidae	codfishes	29	-	42	160	5 cm[p]	juv	trans.
Octopodidae	octopods	27	-	42	90	3 cm[m]	i	unknown
Pandalidae[b]	pandalid shrimp	27	-	24	131	25 cm[q]	i	max
Porichthys notatus[b]	midshipman	27	11,357	39	101	38 cm[i]	sp	max
Onychoteuthis borealijaponicus	boreal clubhook squid	25	8,417	24	59	35 cm[r]	i	max
Salmonidae[b]	salmonids	23	-	58	376	18 cm[f,s]	juv	juv
Trachurus symmetricus	jack mackerel	22	17,771	30	80	6 cm[l]	juv	max juv
Hexagrammidae	greenlings	21	-	36	164	5 cm[p]	juv	set.
Ophidiidae	cuskeels	18	-	27	69	36 cm[i]	juv	max
Sergestidae[b]	sergestid shrimps	18	-	15	61	8 cm[q]	i	max
Atherinopsidae+Atherinidae	silversides	18	-	27	107	44 cm[i]	sp	max
Scomber japonicus	Pacific mackerel	17	13,957	22	47	9 cm[l]	juv	max juv
Pasiphaeidae	glass shrimps	16	-	15	31	8 cm[q]	i	max
Anoplopoma fimbria	sablefish	15	8,095	25	84	50 cm[t]	juv	juv
Icichthys lockingtoni[b]	medusafish	11	2,060	11	13	41 cm[i]	sp	max

[a] Predator count does not account for prey reported at a higher taxonomic level that can't be resolved at the species level, including 1 additional predator for Clupeidae, 2 for Clupeiformes, and 4 for Pleuronectiformes. Thus total predator counts for northern anchovy, herring, righteye flounders, sanddabs, and Pacific sardine may be slightly higher than reported here.
[b] Denotes forage species not targeted in initial literature search that were added based on database analysis
[c] Pacific sardine predator count is likely underestimated due to the extremely low levels of sardine in the ecosystem for several decades ~1955-1985.
[d] Number of predator samples examined only provided when prey taxa were identified to species level in original citations.
[e] Number of predator-prey links indicate the number of times the prey appears in the diet of a predator in the database and serves as an indication of how well studied the trophic relationship is.
[f] Prey size indicates the size at which different prey categories occur as forage in the diet. Prey size is reported for small pelagics as max size of adults, for invertebrates as max size (except for rock crab magalopae), and for juvenile fish as size at settlement, transformation, or juvenile stage, athough these fish may occur at larger sizes in the diets. The CCPDD currently includes prey size data from individual studies for a few commercially important juvenile fish species to distinguish between juvenlie and adult stages including: rockfish 2-37 cm, *Citharichthys* spp. 2-40 cm, Pacific hake 2-70+ cm, and salmon 10-59 cm.
[g] Forage group: i=invertebrate, j=juvenile fish, sp=small pelagic
[h] Love et al. 2002, [i] Eschmeyer and Herald 1983, [j] Décima et al. 2010, [k] Kashiwada et al. 1979, [l] Moser 1996, [m] Markaida 2005, [n] Sakuma and Ralston 1997, [o] Hines 1986, [p] Matarese et al. 1989, [q] Wicksten 2011, [r] Bolstad 2008, [s] Daly et al. 2012, [t] Head et al. 2014

fish with >50 cm total length, and cross-checked the list with natural history guides that were also used to assess the pelagic habits, size, range and diets of the fish (Eschmeyer and Herald, 1983; Love, 1996; Love et al., 2002). Cetacean and pinniped lists were derived from books and websites with range and diet information (Evans, 1987; NOAA, 2014; Riedman, 1990). Jumbo squid range in recent years has expanded to include all regions of the CCS (Cosgrove, 2005).

2.6. Data accessibility

The raw data from the CCPDD used for the analyses in this paper are freely available from the Dryad Digital Repository (Dryad Data Package, 2015; Szoboszlai et al., 2015). Specifically, we include data for predator and prey taxonomy, citation, study location and region, study date and season, observation type, sample size, and consumption units. This data resource will be available to integrate with existing species-interaction datasets (e.g., Global Biotic Interactions (GloBI), Poelen et al., 2014) and into ongoing research and modeling efforts that integrate diet data (e.g., Atlantis and Ecopath models of the California Current).

3. Results and discussion

3.1. Spatial and temporal overview of CCS diet data

At 67% inclusion, or 193 of 285 known citations, the CCPDD represents the most comprehensive compilation of historical information published on predation of forage species in the California Current, and the first effort to assemble over 100 years of data for all available species of middle- to upper-trophic predators in a database format. The CCPDD compiles diet data on 119 upper-trophic level pelagic predators of forage species found in the CCS from 1893 to 2012. This includes 39 of 58 bony fish species (67%), 15 of 19 cartilaginous fishes (79%), 37 of 53 seabirds (70%), 21 of 26 cetaceans (81%), six of six pinnipeds (100%), and one invertebrate, the jumbo squid (detailed lists of predator species with diet data are in Appendix A, and predators without diet data are in Appendix C). Overall, information was synthesized for over two-thirds of the predator species in the CCS, and the missing species represent gaps in information due to the absence of previously-published data for these predators. Data availability is likely related to the abundance of the predator and prey, since more common or widely distributed species are perhaps more likely to be encountered by predators or researchers. Although we conducted thorough searches of the published and gray literature for predator diet data, many species are likely represented in unpublished data sets not included in the CCPDD.

A regional breakdown of studies by location indicated that fish predator diets of forage species were equally well-studied across the range of the CCS, seabird predator data came primarily from localized breeding locations aggregated within states, and marine mammal diet data were mostly from central and southern California (Fig. 1a–c). Across all major taxonomic predator groups, published

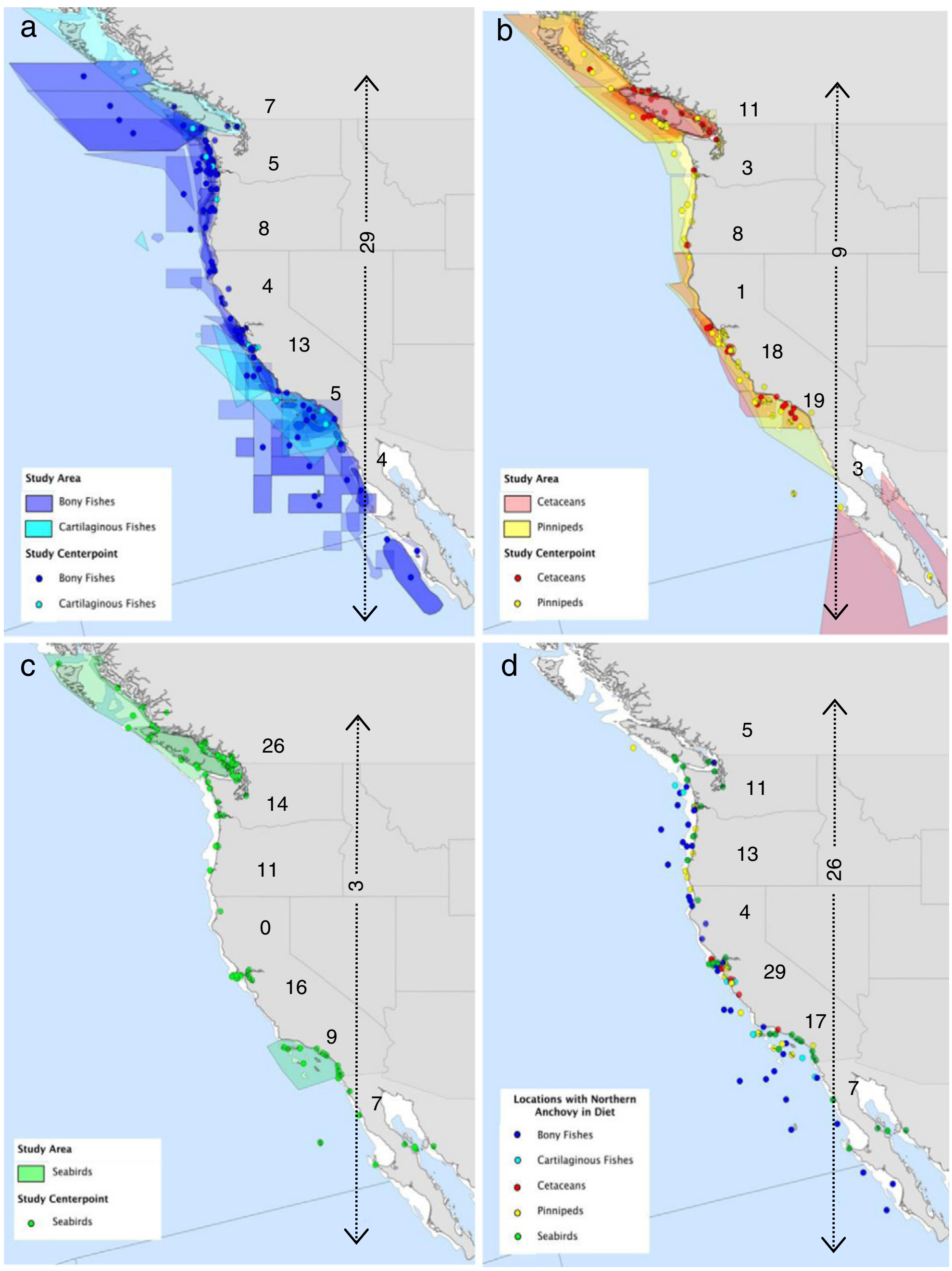

Fig. 1. Distribution of study locations for three major predator groups: a) large fishes, b) mammals, c) seabirds. Points indicate the center of the study area, shaded areas represent the total study area. Panel d) shows the distribution of diet data available for predator consumption of northern anchovy, broken down by major predator groups. Number of citations are reported on each map, broken down by regional geo-political boundaries: Canada, Oregon, Washington, northern California, central California, southern California, and Mexico. Numbers with arrows indicate the number of citations from large-scale studies that spanned more than one region. In some regions, studies included averaged data from both inside and outside the typical CCS limits (fish and seabirds to the north, cetaceans to the south). Data from inland seas (e.g., Strait of Georgia, Puget Sound, Gulf of California) or river mouths were included when CCS data were not available for that region.

data from Mexico were limited, as were studies in northern California and southern Oregon. Some of the regional data gaps related to limitations imposed by the biology of the organism. For example, diets of nesting seabirds can be readily assessed through direct observation and, as such, studies are restricted to breeding areas. Data are lacking for offshore species that do not breed in the CCS and which would require lethal gut-sampling or stomach lavage to gather diet data. Likewise, pinniped diet was well-represented in some regions because these animals haul out on the shore, allowing access to diet information from scats, and poorly studied in more remote areas less accessible to researchers (northern California and southern Oregon). Diet data for protected species such as cetaceans were limited to mostly opportunistic sampling of beached or net-caught animals, resulting in small sample sizes without robust regional representation. Data “hotspots” were concentrated around research institutions such as those near San Francisco and Monterey Bay. Studies of central and southern California cover high numbers of predator species, in contrast to Mexico, which is more data-poor. This data gap is likely due to accessibility, language barriers, English search terms, and limited access to published materials from Mexico.

To highlight the potential for the database to portray spatial information about consumption, we queried the CCPDD for all predators that ate northern anchovy, an important forage fish in the diets of many predator groups across the extent of the CCS (Fig. 1d). We selected northern anchovy because it was the highest single species prey taxon with the largest number of predators, after the aggregate prey group for juvenile rockfish (Table 2). This type of information, in combination with the spatially explicit data for each diet study's location, summarizes visually the occurrence of particular forage taxa in diet studies. The prominence of northern anchovy in the diet of CCS predators across all taxonomic groups and regions supports its role as a critical forage species in this ecosystem. Further investigation of the spatial and temporal variation in the amount of northern anchovy in these diets, and assessments of other priority forage species will provide the information needed to assess the role of forage species in nearshore food webs.

The CCPDD also offers insight into the timeline of data published on the predation of forage species (Fig. 2). Not surprisingly, diet data from the past 50 years existed for most predator species, with peaks in the mid-1970s to 1980s and mid-1990s to 2000s. Older records tended to represent only a few predator species, for example, long-term records of marbled murrelet diet derived from stable isotope analysis of feathers from museum collections, or records of marine mammal diets from whaling industry data.

3.2. Forage taxa ranking

Our data synthesis identified 32 taxa that met our criteria for consideration as a forage species outlined above, based on occurrence in predator diet, small size, low trophic level, pelagic habits, and a range primarily in the CCS (Table 2). Forage taxa with the highest number of predators, in descending order, were: rockfishes, anchovy, krill, herring, and market squid (51–61 predators), followed by right-eye flounders, lanternfishes, sanddabs (left-eye flounders), sculpins, gonatid squid, surfperches, Pacific hake, Pacific saury, smelts, Pacific sardine, and Pacific sandlance (32–41 predators; detailed predator lists for each forage taxon/taxa are in Appendix D). Comparisons among forage taxa were confounded by the need to group some species at the genus level or higher, while others remained as individual species. A ranking of the highest number of predators for individual forage species yields anchovy as the single top forage species in the CCS, followed by herring and market squid. For each forage taxa, we provide lists of predator species that consumed it, information not previously compiled for the CCS (Appendix D).

3.3. Predator diet data

3.3.1. Observation type

The majority of observational data on predator diet of forage taxa in the CCPDD were derived from predator stomach-content analysis (53%), particularly for bony and cartilaginous fishes (100%) and cetaceans (72%) (Fig. 3a). However, for some taxonomic groups of predators, published diet data came almost exclusively from bill loads (85%, seabirds) or scats (80%, pinnipeds) because their diets can be sampled nondestructively and these animals are protected. Diet data derived from stable isotope analysis were rarely included in the CCPDD because the taxonomy of the prey was poorly resolved or because consumption was not measured as a proportion of total

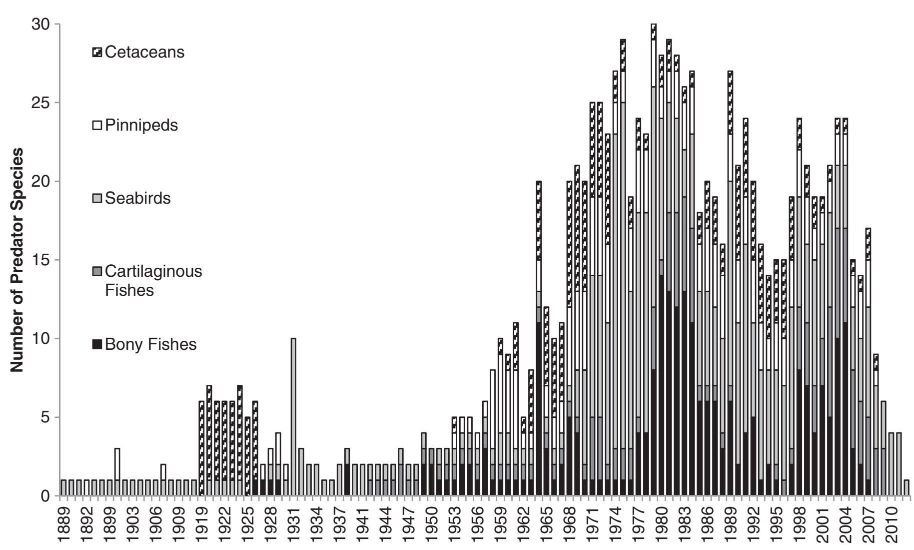

Fig. 2. Timeline of available data summarized by number of predator species with forage species in their diet, broken down by major taxonomic group. Individual year does not necessarily indicate discrete data for that time period because many studies presented data averaged across multiple years. To assess time frame of diet data available for individual species, see Appendix B (summarized range of years) or Supplement 1 (years or year spans).

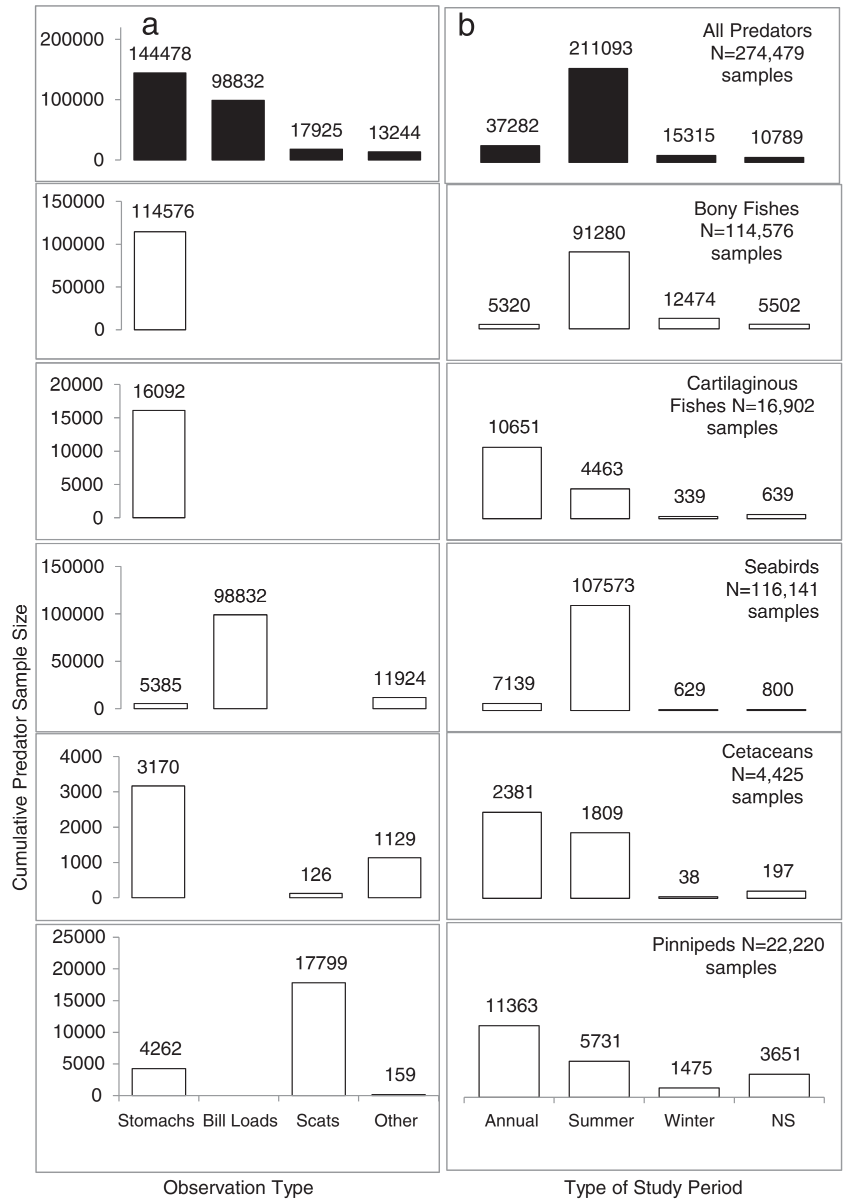

Fig. 3. Data summaries based on cumulative predator sample size: a) for different observation types, b) for annual vs. seasonal study periods. For observation type, other = chemical analyses, dip or tow net, dropped pellet, visual observation; for study period, annual represents >12 months, summer = April–September, winter = October–March, NS = non-seasonal data averaged across fewer than 12 months. Dark bars summarize all predators; white bars summarize individual taxonomic groups.

consumption. Data needed to be in percent mass or percent number for comparison with other diet studies. However, we chose not to exclude all stable isotope data from the CCPDD because in some instances it was the only type of data available for a predator species.

The likelihood of detecting a predation event depends on the method of observation and traits of the taxonomic group being observed (reviewed by Pierce and Boyle, 1991, for marine mammals, Hyslop, 1980, for marine fishes, and Duffy and Jackson, 1986, for seabirds). Observations from stomach contents can be biased toward animals that can be more easily caught live, such as fish. Stomach contents from marine mammals, found as dead or stranded animals may oversample abnormal feeding by sick animals and age-specific mortality patterns may not be indicative of the general population. Bill load observations have prey identification biases influenced by the daylight level, colony visibility and distance, and observer ability (Elliott et al., 2008). Additionally, studies may or may not include numerical and/or digestion correction factors, which affect estimates of number and size of prey consumed (Sweeney and Harvey, 2011). These biases associated with the different data collection methods may influence the ability to directly compare among samples and taxonomic groups without data using various approaches.

3.3.2. Seasonal vs. annual data

Most data on predator diet came from samples collected during the summer season (77%), whereas winter sampling was more restricted (6%) (Fig. 3b). For cartilaginous fishes, cetaceans, and pinnipeds, more data were presented at an annual rather than seasonal level, whereas observations on seabirds and bony fishes were almost exclusively made during summer. The major gap in availability of winter data was expected given the difficulty of sampling during stormy winter weather and the absence of seabirds at breeding colonies. That data for some predators were presented primarily at an annual level is likely a reflection of the difficulty of sampling some taxa and the subsequent combination of data over longer-than-seasonal time periods. For example, the low sample sizes of diets of predatory cartilaginous fishes and marine mammals reflect the

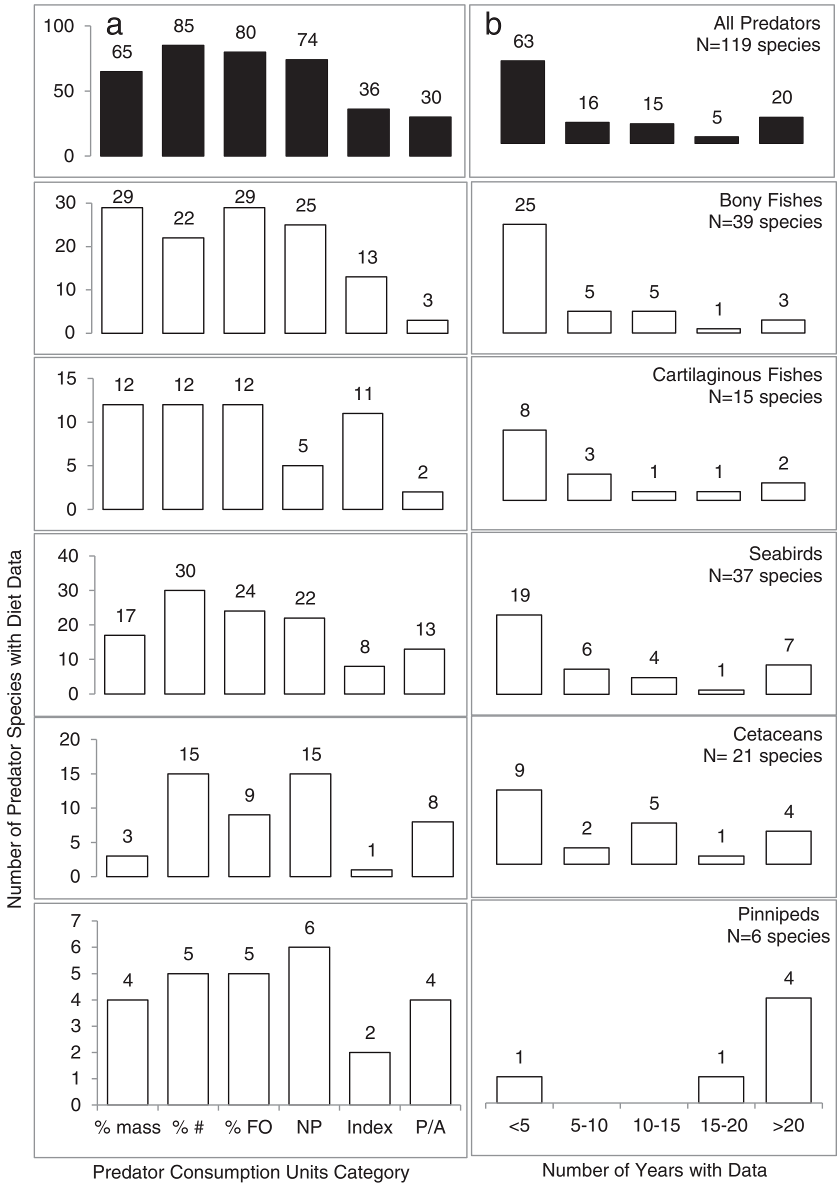

Fig. 4. Data summaries based on number of predator species with diet data in the CCS: a) types of predator consumption units, b) number of years with data. For predator consumption units, % mass also includes observations based on % volume, FO = frequency of occurrence, NP = non-proportional data that could be converted to %, Index = non-dimensional data, e.g., Index of Relative Importance (IRI), P/A = presence/absence data. For number of years with data, data averaged across multiple years are treated as individual years. Dark bars summarize all predators, white bars summarize individual taxonomic groups.

challenges associated with capturing diet information from wide-ranging and protected species.

3.3.3. Units of consumption

Within each predator taxonomic group we characterized the types of data used to portray the amount of forage consumed by pelagic predators. These data included summaries of proportional and non-proportional data for prey mass, volume, number, and frequency of occurrence (FO), as well as presence/absence data. Across all taxonomic groups, prey data that were proportional by number were available for the most predator species (71%) (Fig. 4a). Otherwise, within each major taxonomic group, proportional data were fairly evenly available across the different methods for quantifying consumption, except for cetaceans which had relatively limited data as % mass. Fish predators, sampled primarily by stomach content analysis, comprised the most species with percent mass data (63% of all predators, 75% of fish predators). Seabirds were generally restricted to percent number data because most prey were sampled by visual observation of adults feeding chicks. Although 46% of seabird predators had percent mass data, sample sizes for these studies were low compared to sample sizes of studies with percent number data. All taxonomic groups had high numbers of predator species with raw, non-proportional consumption data that could be transformed into percentage data if sample size was provided. Different methods for measuring consumption among taxonomic groups can complicate comparisons and data compilation for use in models.

3.3.4. Short vs. long-term data

More than half of the predators studied had limited temporal records, represented by fewer than 5 years of data, and only 20 predator species had over 20 years of data across all published studies (Fig. 4b). Within each taxonomic group, very few predator species had long-term records (>5 cumulative years with data), with the

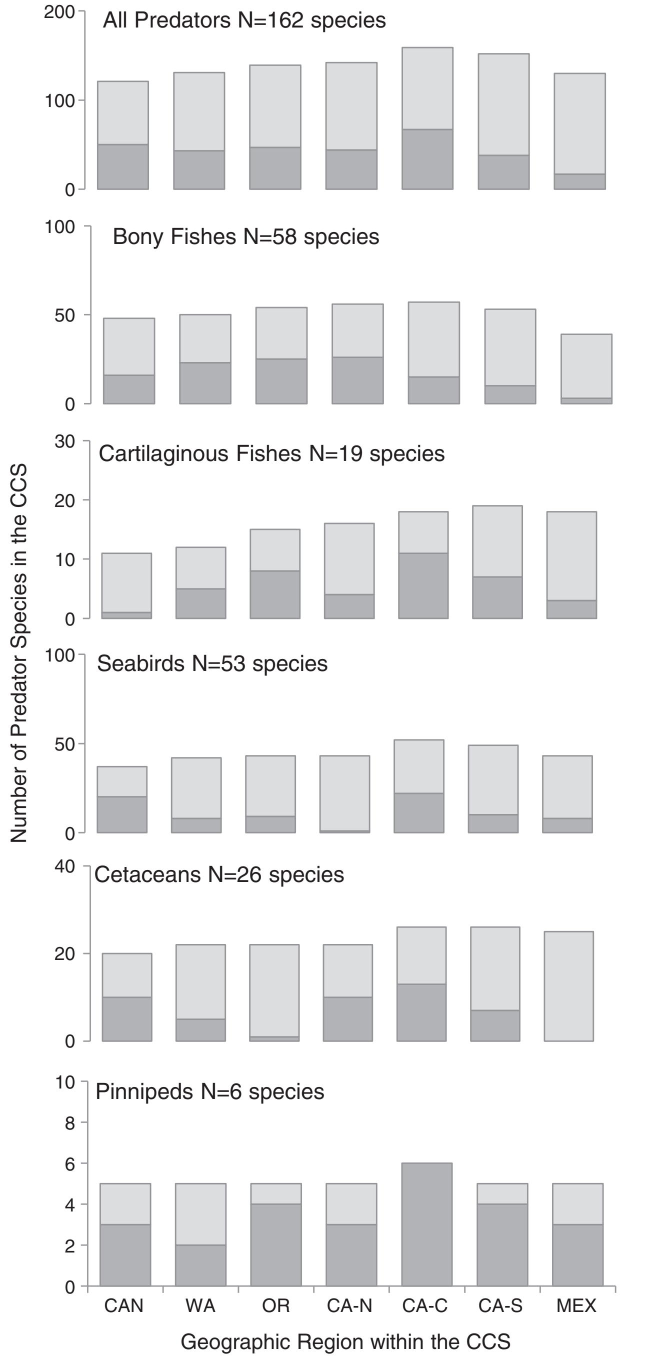

Fig. 5. Data summaries based on number of predator species occurring in the CCS. For geographic region with data, CAN = Canada, WA = Washington, OR = Oregon, CA-N, CA-C, CA-S = northern, central, and southern California, respectively, MEX = Mexico. Dark gray bars indicate the number of predator species with diet data in each region, light gray bars indicate the number of predator species without diet data. Although the majority of predators do not have diet data in a specific region, many of them have diet data for another region of the CCS.

exception of pinnipeds and seabirds. The limited availability of long-term studies is a known constraint in developing ecosystem-level food web models (Field and Francis, 2006; Pikitch et al., 2014). The fragmented nature of the temporal record for individual predator species limits the detection of predator response to long-term environmental change (Ducklow et al., 2009) (Supplement 1). Even species with long-term records often have data reported as multi-year averages of annual data, obscuring the inter-annual variation key to long-term change analyses.

3.3.5. Regional data

The regional availability of data varied by major taxonomic group of consumers, with the most bony fish predator species sampled in Washington, Oregon and northern California, and cartilaginous fishes, seabirds, cetaceans and pinnipeds in central California (dark gray bars in Fig. 5). Although central California had the highest number of predator species with diet data (67), it also had the highest number of middle- to upper-trophic-level predator species that occur in any one region (159 of 162 species for the entire CCS, light gray bars in Fig. 5). Thus the availability of data for a greater number of predator species in central California may indicate that this is the center of distribution for CCS predator diversity, including both northern and southern predators, or it may be a sampling bias. Overall, no one region had data for a majority (>50%) of the predator species that occurred there. Notable information gaps existed for most species in Mexico, seabirds in northern California, cetaceans in Oregon, and cartilaginous fishes in Canada. Regional data gaps or hotspots could result from literature searches conducted in English, not Spanish, some regions being more isolated or remote making it difficult to access breeding colonies for diet collection, and researchers conducting studies near their home institutions. For example, central California includes over 50 marine science research institutions and private groups, which could influence the comparatively high number of diet studies in this region (NOAA, 2015).

3.3.6. Spatio-temporal data gaps

To understand the interaction between spatial and temporal gaps in the CCPDD, we explored how many predator species had data representative of each year and region (Fig. 6). This detail highlighted regional and historically rich “hotspots” with data for more than 10 predators in the same place and year, including central CA in the early-1970s, and WA and OR in the early-1980s and mid-1990s to mid-2000s. During nearly all the years since 1950, each region had at least one to three predator species with data, indicating the breadth of data housed in the CCPDD, However, this breadth is relatively shallow in terms of predator species richness, since most of the time, and in most regions, fewer than six predator species had diet data. The distribution of these spatio-temporal gaps and “hotspots” highlights when and where published diet data exist. This summary will be useful to understand the availability of data for evaluating long-term and regional changes in the prey species in the CCS.

3.4. Individual predator species

We synthesized available data for each predator species to highlight gaps in the data as well as specify areas for further analysis and research (Appendix B has predator-specific metrics, Supplement 1 has temporal availability of data, Supplement 2 has regional availability of data). Strong candidates for more in-depth analyses met criteria for good spatio-temporal resolution (missing only three regions within the species' range, >20 years of data), and large overall sample size, number of predator-prey links, and number of citations (>1000 samples, >30 predator-prey links, >3 citations) (Table 3). Seabirds and pinnipeds comprised two-thirds of this list, most likely due to the ease of sampling these species in the nearshore. The bony fishes on this list (Pacific hake, Chinook salmon) are the target of major commercial fisheries.

4. Conclusions

The immense data synthesis that comprises the CCPDD provides evidence for the role of a diverse range of forage taxa in the diets of predators near the top of the California Current marine food web. The analysis of numerous predators consuming a large variety of forage taxa indicates a complex, interconnected food web. Energy transfer in the CCS occurs via a range of pathways, highlighted by the existence of many intermediate trophic level taxa, as opposed to other upwelling systems characterized

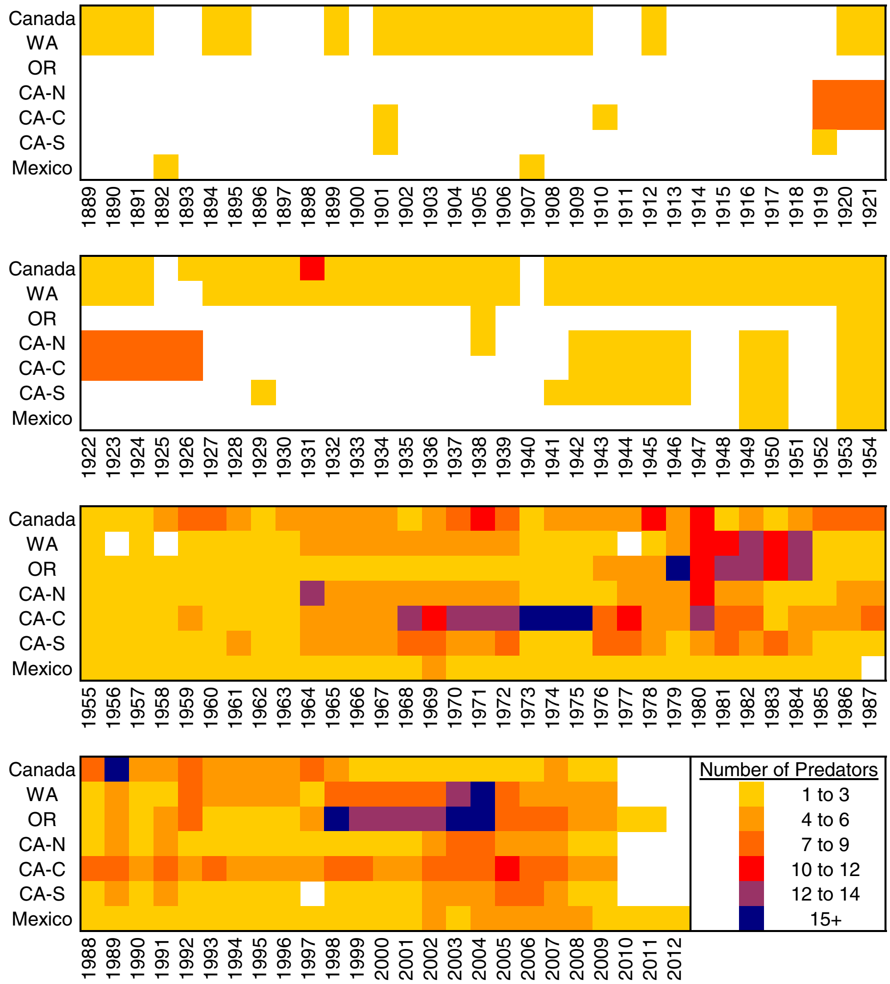

Fig. 6. Total number of predator species with diet data by year and region.

as "wasp-waist", where energy transfer occurs via a few intermediate species (Cury et al., 2000; Freón et al., 2009). Management of such complex systems is challenging because as more species are involved, models and predictions of future communities and interactions become increasingly uncertain. Likewise, when the diversity of forage species is high, the ability to predict predators' responses to their prey is reduced because prey species have individualized responses to spatio-temporal changes in ocean conditions. Furthermore, predators can have functional responses to changes in the relative abundance of their prey that are not directly proportional to prey abundance in the system.

Information housed in the CCPDD will support the management of forage taxa. Some of the highly-ranked forage taxa are already managed (e.g., market squid, krill, sardine), whereas others are not (e.g., myctophids, gonatid squid, saury, smelts), or do not have recent assessments (e.g., anchovy). While prey taxa such as rockfish and hake may be managed as adults, the database captures the importance of the

Table 3
Top predator species with >1000 samples, >30 predator-prey links, >3 citations, majority of regions (not missing more than half of the 7 CCS regions that are within its range), and >20 years sampled.

Scientific name	Common name	Cumulative sample size	Number of predator-prey links	Number of citations	Total regions (regions in range)	Span of years (total # years)
Merluccius productus	Pacific hake	54,011	515	8	6 (7)	1964–2004 (23)
Cepphus columba	Pigeon guillemot	33,007	122	6	3 (6)	1931–1997 (28)
Uria aalge	Common murre	29,889	704	15	4 (5)	1931–2011 (43)
Zalophus californianus	California sea lion	12,318	622	15	4 (7)	1901–2006 (42)
Oncorhynchus tshawytscha	Chinook salmon	7,741	395	7	5 (6)	1926–2007 (27)
Phoca vitulina	Harbor seal	6,383	348	12	5 (7)	1927–2008 (35)
Cerorhinca monocerata	Rhinoceros auklet	6,225	719	18	3 (6)	1974–2007 (28)
Ptychoramphus aleuticus	Cassin's auklet	2,189	204	8	3 (5)	1977–2007 (23)
Eumetopias jubatus	Steller sea lion	1,674	254	7	4 (5)	1901–2007 (36)
Phalacrocorax auritus	Double-crested cormorant	1,117	115	7	5 (7)	1931–2011 (24)
Prionace glauca	Blue shark	999	63	6	6 (7)	1974–2009 (23)

juvenile stages as forage. Comprehensive lists of which predators eat high-ranking forage species were previously unavailable; this information improves our collective understanding of the role of individual forage species in the food web. This synthesis of information on forage taxa in predator diet combines diet data for individual predator species into a publicly available database and comprehensive assessment of forage in the entire CCS community of middle- to upper-trophic predators, across space and time. In this way, individual datasets can be leveraged as a whole to inform more coordinated management of economically valuable forage and predator species.

The process of compiling information from such a wide variety of sources revealed some key challenges of data synthesis. Methods of data collection and reporting varied by taxonomic group. To synthesize data for all forage consumers, those differences required reconciling the limitations of different data (Young et al., 2014) with the need to compile information across all taxonomic groups. A standardized method is needed to deal with the range of information that has been reported, including the use of different consumption units, varied data quality (e.g., sample size), predator ontogeny, and differences in temporal and spatial averaging of diet data. Because food web models generally track patterns in predator-prey biomass, data as biomass are the most useful for this application. However, some major taxonomic groups, such as seabirds, have mostly percent number data that cannot always be easily integrated with percent mass data. Prey mass from these diet studies can only be estimated using prey size data, which should be collected simultaneously. Prey in seabird diets can also be characterized qualitatively, e.g., percent number can be used as an approximation of biomass when prey are known to be of similar sizes. Ecosystem-level models will benefit from integrating higher-resolution diet data into their predator-prey interactions, but must reconcile differences in consumption values among major predator groups to be able to utilize much of the prey data that are based on numerical instead of biomass consumption units.

Taxonomic, spatial, and temporal data gaps were discovered by reviewing the collective data on predator diet. The absence of published diet information for one third of upper-trophic-level predators in the CCS, and very few citations for many others, begs for additional data compilation, including publication of existing raw datasets (Appendix C). Regional gaps indicate that "borrowing" data from predators studied in neighboring regions will be required to develop a broad picture of ecosystem processes. However, predators for which high-resolution spatial data exist indicate that some predators have significant spatial variation in diet, so this approach should be used with caution. Temporal gaps, evidenced by minimal data from winter, hinder seasonal inferences about predator diet, yet seasonal differences in prey availability and energy density are known to affect predators. Some data gaps derive directly from difficulties associated with collecting the data (e.g., remote locations, extreme weather), whereas others gaps are a function of the ecology of the system (e.g., some species have small/low-density populations or do not feed in the CCS in certain seasons). Review of these gaps can inform the siting and timing of future studies, particularly at the level of individual predator species, as well as the inference space for modeling studies.

Evaluation of the database and its summaries of existing data highlight a way forward by identifying key species with robust data that are well represented regionally and temporally. Data for well-studied predators can be summarized for high-resolution insights into temporal-spatial variability in predator reliance on forage species. Predator consumption of key forage taxa (e.g., anchovy) can be summarized for the full group of CCS predators to chronicle the pressure predators exert on economically important forage taxa. In the past, information on predator diet in the CCS available to stakeholders has been restricted in terms of taxonomic, spatial and temporal resolution. With recent advances in the integration of relational databases, separate studies have been synthesized to reflect a more complete picture of the California Current pelagic marine food web. By utilizing the CCPDD to assess the extent of data available on consumption of forage taxa by individual predators, future research can target discontinuities in the collective understanding of predator-prey interactions in the California Current, building a more robust portrayal of these food webs. Similar approaches can be used in data-poor systems to guide research plans.

Databases such as the CCPDD support a culture of data-sharing among research scientists. They facilitate standardization of research data and simplify access to queries for extracting information, providing a conduit between research data and end-users. Food web research would further benefit from an expansion of the data-sharing culture. Many of the studies contained within the CCPDD present averaged data that obscures small-scale spatio-temporal patterns; access to the data in a raw format would facilitate finer-scale and longer-term analyses. Some disciplines, such as fish diet studies, already embrace this tactic as evidenced by the inclusion of raw data as appendices. Future research and reports of predator diets should strive for standardized data collection, compilation, and reporting of raw data in appendices, preferably in digital, machine-readable formats, so that this valuable information can be more easily compiled, shared, and re-analyzed to improve our understanding of marine ecosystems.

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